

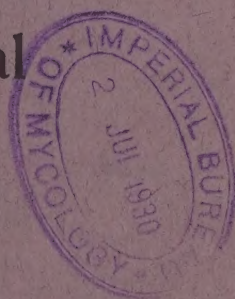
CONFERENCE OF EMPIRE METEOROLOGISTS,
1929.

AGRICULTURAL SECTION.

Agricultural Meteorology

In its

Plant Physiological
Relationships.



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AGRICULTURAL METEOROLOGY IN ITS PLANT
PHYSIOLOGICAL RELATIONSHIPS.

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Agricultural meteorology is the study of the effects of meteorological conditions on plant yield. Yield, with which the practical man is alone concerned, is, of course, the final expression of the integration of the whole complex of physiological processes of the plant. One is dealing with a very complex system in which the physiological processes of the plant react with the external conditions. Meteorological conditions such as temperature, light intensity humidity of the air, since they produce a marked effect on the rate of important physiological processes in the plant, are often termed "factors"; we speak of the growth of a plant being controlled by a temperature factor, a light factor and so on. These meteorological factors for the most part vary continually during the growth of the crop, which may last over many months or even years.

One of the central problems of plant physiology is the elucidation of the effect on the plant of the external factors of the environment and of these the meteorological factors are not the least important. The problem is one of great difficulty. In the first place a living organism is an exceedingly complex system and one which is highly integrated. The various processes on which the life of the organism depends are very closely co-ordinated and, indeed, are necessarily so if its life is to continue. It follows that a change in one process in the plant may markedly affect the rate of other processes; thus it is hard to distinguish between primary and secondary effects.

There is in addition a second complication which shows itself even in the study of a single physiological process. This complication is the high "interrelationship" of the factors affecting such a process. The effect produced by any one factor is markedly dependent on the intensity of other external factors. Thus, if we are considering the effect of the sun's radiation on the rate of sugar formation in the leaf we find that the effect produced varies with the temperature of the leaf and the concentration of carbon dioxide available. If the temperature is low a doubling of the light intensity will have only a slight effect, while with a higher temperature the effect will be greatly enhanced. The close interrelationship of factors is one of the chief lessons of more recent physiological work,

but one which makes much more intricate the study of the effect of meteorological conditions on plant processes such as growth.

In the third place the variation of the environmental factors—especially the climatic factors—from day to day, from hour to hour and even from minute to minute, adds another difficulty to the interpretation of crop yield in terms of the effect of such factors on the physiological processes of the plant.

It must also be pointed out that there is often a considerable lag in the action of a climatic factor and the appearance of the resultant change in the plant. Crop yield may be largely determined by a bright period or a period of rainfall which occurred long before; we have a process known as physiological predetermination.

As has already been stated, the contribution which plant physiology can make to agricultural meteorology consists in analyses of the way in which climatic factors affect crop yield. This analytical problem can be attacked in three ways. In the first place the plants may be studied under *field* conditions, various physiological processes, such as rate of increase of dry weight, rate of increase of leaf area, rate of assimilation and respiration being followed *throughout the growing season*. Work of this kind is very laborious and, owing to the large variation of plants grown under field conditions large samples have to be collected to obtain significant results. A full field experiment of this kind has not yet been carried out.

In the second way the experimental technique is simplified by growing the plants in pot-culture in the open. The plants are thus exposed to natural climatic conditions and the correlation of their various physiological processes with climatic factors can thus be determined. The most elaborate study of this kind is that of F. G. Gregory referred to below.

The third mode of attack is a study in the laboratory of the effect of various climatic factors such as temperature, light, humidity, on the growth and other processes of various plants or plant organs. Useful knowledge may be obtained in this way, but owing to the interrelationship of factors referred to earlier and the high integration of the plant body it is difficult from a study of the effect of a single factor on single organs to deduce the action of a complex of meteorological factors upon the plant as a whole.

Correlation between the Intensity of Climatic Factors and the Growth of Plants.

The only elaborate investigation that has been made of this relationship is the study of barley by Gregory in the years 1921–1924 (*Annals of Botany*, XL, 1–26, 1926). As already stated, the plants were grown in pot-culture, the water-content of the soil being kept up to a lower limit by artificial supplies though this limit was exceeded in periods of rainfall. Seven environmental factors were

recorded during the experimental periods of each of the four years, namely, maximum day temperature, average day temperature, minimum night temperature, average night temperature, total radiation (calories per cm.² per week), hours of bright sunshine, and evaporating power of the air. Three physiological processes of the plant were measured, namely, net assimilation rate, relative rate of growth of leaf surface, and relative rate of increase of dry weight. Owing to the high correlation of the external factors (solar radiation and temperature, for example, tend to vary together) partial correlations had to be determined. It was shown that the net assimilation rate had a high partial correlation with day temperature and with radiation, and this was *positive*, while there was high *negative* correlation with night temperature. This last result is to be explained by the fact that a high night temperature pushes up the rate of respiratory loss and so reduces the rate of *net* assimilation.

A partial positive correlation of relative leaf growth with average day temperature was observed and a negative correlation with night temperature, and also a large negative correlation with total radiation. The fact that the correlation with total radiation is positive for net assimilation but negative for relative leaf growth rate tends to keep the yield constant. High radiation will tend to reduce the rate of leaf-area growth but compensation will occur since the high radiation will increase the assimilatory efficiency of each unit of leaf-area.

It is clear from the few results that have been quoted that the method employed by Gregory is a very fruitful one. Much light could be thrown on agricultural meteorology by an extension of this method. By growing one or more crop plants in exactly similar pot-cultures in localities with widely different meteorological environments and determining by the method of correlation the reaction of the plants to the various climatic factors very valuable knowledge would be obtained.

In the third method of attack on the physiological problems of agricultural meteorology the effect of the various climatic factors on the plant processes is investigated. It will be useful then to give a brief survey of the action of these factors on the plant.

Effect of Temperature.

The question of how to summate temperatures so as to relate them most satisfactorily to their effect on plants has been a burning one in plant geography for a very long time and a similar problem arises in relation to plant physiology. De Candolle as long ago as 1874 divided the earth into temperature zones, the lowest having the temperature of most months below 0° C., and the vegetative period for plants between 0° and 5° C.; the other zones had mean

temperatures of 0-14° and 15°-20° and the zone of highest temperature about 25° C. A great flaw in the system of De Candolle was the complete neglect of yearly periodicity which plays such an important part in the life of plants in temperate regions. Koppen improved on the system of De Candolle by defining the cold zones as those with one to four months with a temperature over 10° C., and later he related his zones to the position of the isotherm 18° C. during the coldest months and the isotherm 22° C. for the warmest months.

It is obvious, however, that in addition to the length of the period of growth the duration of high and low temperatures must be considered. Some authors accordingly summate in temperature hours over the whole year or for the frost-free period. Livingston and Shreve (*Publ. Carnegie Institution, Washington, No. 284, 1921*) take into account the number of frost-free days during the vegetative period and summate the temperatures in these and determine also the number of days with a temperature over a definite level. Vahl takes the mean temperature of the coldest month and the mean temperature of the warmest month and from them constructs a formula, as does also Samuelsson. With such formulæ they have been able to correlate with temperature the northern limits of wheat in Europe and Siberia, and also the distribution of the hazel.

Though some slight success may be obtained in this way in correlating temperature with the distribution of some plants, it is evident that a formal treatment of this kind is doomed to failure when a living organism such as the plant is in question. If we wish to determine the activities of the plant in terms of temperature, it is evident that we must use physiological data which embody the response of the plant to such a meteorological factor. Livingstone and Shreve (*loc. cit.*) were the first to attempt to use physiological data in climatological work. They weighted their temperature averages according to the growth rates of plant organs which had been observed at different temperatures under laboratory conditions. This method however, had not much success in determining plant distribution and this is not very surprising. Growth data of this kind are not available for many plants and they refer usually to particular parts of the plant such as the root and not to the plant as a whole. Apart from this, however, there is the strong objection to the method itself that it uses physiological data which relate temperature merely to the *growth* of the plant. There are, however, other processes in the plant, such as assimilation and respiration, which are of equal or greater importance for its development, but unfortunately these may have a markedly different response to temperature than the mere elongation of the plant which is usually considered as growth. The evident need is for temperature curves of all three processes of assimilation, respiration and growth so that the effect of temperature on the plant as a whole can be accurately determined, though there must, of course, be other processes in the

plant whose response to temperature is different from that of any of the three processes just mentioned.

How different are the responses of growth, assimilation and respiration is shown by the graph below which gives the relationship between temperature and rate of growth in length of the shoots of maize seedlings, and Table I, after Lundegårdh (*Biochem. Zeit.* 154, 213, 1924), which indicates the effect of temperature on the rate of the processes of respiration and assimilation of the leaves of the potato plant.

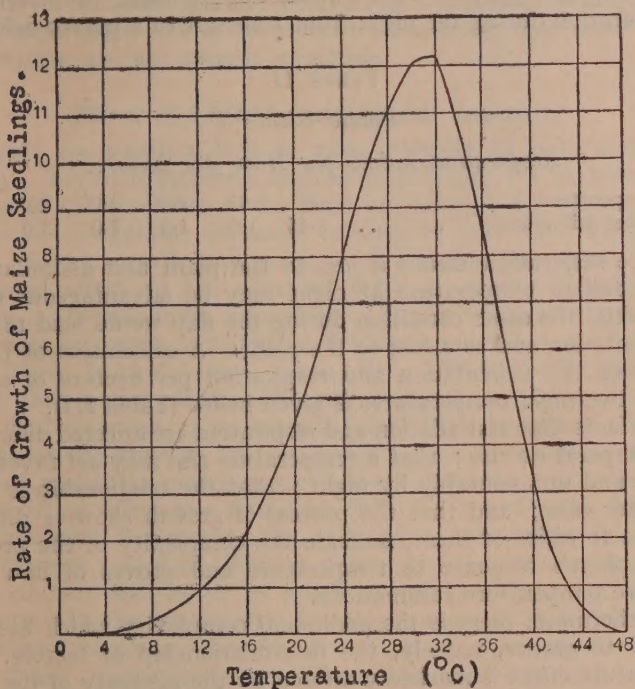


TABLE I.
Effect on Rate of Assimilation and Respiration of Raising
Temperature 1° C.

Temperature ..	5°	10°	15°	20°	25°	30°	35°	40°	45°	49°
Respiration ..	1.08	1.08	1.06	1.10	1.07	1.07	1.06	1.29	1.01	1.46
Assimilation—										
With full light ..	1.27	1.25	1.08	1.08	0.96	0.92	0.81	—	—	—
With 1/25 light ..	1.18	0.95	0.90	1.52	0.79	1.00	—	—	—	—

Such a graph and such table show how futile is a mere summation of temperatures, for the effect of a given rise of temperature may be very different at different temperature levels. Thus, at 5° C. an

increase of temperature of 1° increases assimilation (at high light intensity) by 27 per cent., while a similar rise at 15° C. increases the rate of the process by only 8 per cent. The table also shows that assimilation and respiration respond differently to variations of temperature. It is of course only the *excess* of material formed in assimilation over that lost by respiration that is available for the growth and development of the plant. At higher temperatures the amount lost by the respiration of the plant may be in excess of that gained by assimilation. How large respiration losses may be is shown in Table II, also from Lundegårdh, showing the *hourly* loss by respiration during the night from 1 hectare of a potato field.

TABLE II.

*Potato Field.**Respiration Losses per Hour per hectare.*

Temperature	0°	5°	10°	15°	20°	25° C.
Losses (kilograms)	0.45	1.0	1.5	2.0	3.0	4.5

Since respiration means a loss to the plant and assimilation a gain, a fall of temperature at night may be advantageous to the plant while the same condition during the day would lead to a fall in assimilation and so a loss to the plant. A calculation of Lundegårdh's of the assimilation and respiration per hectare of an oat field at two *night* temperatures is given below (Table III).

The facts that assimilation and respiration are affected differently by a temperature rise; that a temperature rise may act favourably by day and unfavourably by night; that the relationship is linear in neither case; and that the process of growth shows a different response to *either* of these, indicate the complexity of the problem of the plant's response to temperature and proves of how little value are temperature summations.

Furthermore, there is the additional complexity which has been referred to earlier, namely, the interrelationship of factors. The temperature effect is markedly altered by the intensity of the other factors. As Table I shows, the effect on assimilation of a rise of temperature is in general less (as would be expected) when assimilation is kept low by a feeble light intensity than under conditions of high illumination. A fall of temperature of 10° C. at night may thus increase by 30 per cent. the total material available for the plant in that period, as Table III shows.

TABLE III.

*Oat Field.**Assimilation and Respiration per hectare.*

<i>Assimilation.</i>	<i>Respiration.</i>	<i>Gain.</i>
300 kg.	175 kg. (20° C.)	125 kg. (300-175)
300 kg.	132 kg. (10° C.)	168 kg. (300-132)

With reference to the effect of temperature on crop yield the meteorological data of air temperatures are probably as accurate and as complete as can be desired. The plant physiologist, however, can only make full use of them when more physiological data are available as to the effect of temperature and change of temperature on various plant processes, such as assimilation, respiration, growth, flower production, etc.

From the agricultural point of view the temperature of the air is of high importance, but that of the soil, which controls the temperature of the underground portions of the plant, is probably of equal importance. It is unfortunate, therefore, that data of soil temperature are not usually available.

Effect of Light : Quality and Intensity.

Plants are sensitive both to total intensity of light and to its quality. For some processes, such as assimilation, the less refrangible portion of the spectrum is the more important ; for others, as the process of elongation, the more refrangible rays have the greater effect. Plant growth and crop yield are thus the result of the integrated effect on the plant of light of varying intensity and quality. The minimum intensities of daylight under which plants can live is, of course, variable for different species, but is remarkably low. Thus, Shirley (*Amer. Journ. Bot.*, XVI, 354-390, 1929) has shown that many plants will grow under illumination from gas-filled electric lamps of an intensity less than 40-foot candles and buckwheat will grow at 25-foot candles. Sunflower is much more exacting, requiring considerably higher intensities. An interesting compensation effect was found by this observer, for the lower the light intensity the greater the chlorophyll content of the leaves. The response varied in different plants, but the increase in chlorophyll content was never as great relatively as the fall in light intensity. In the hog peanut (*Amphicarpa monoica*), which showed the largest response, the concentrations of chlorophyll were 3.1 and 1.2 mg., respectively, per 100 cm.² for light intensities of 1 per cent. and 71 per cent. of full daylight.

It must be pointed out that though " hours of bright sunshine " are well correlated with " total radiation " (as measured, for instance, by the Callendar Recorder), yet the mere duration of sunshine without any measure of its intensity is very unsatisfactory for plant physiological work. A record of total radiation is certainly an advance over hours of sunshine, but, since it is the luminous rays that are important in plant processes, a measure of changes of brightness throughout the day would be the most valuable.

The effect on plants of light of different quality is still a field in which we have little knowledge, though it is certainly of great importance. It is known, as stated above, that the red orange rays are the more important in the assimilation of plants and the blue

end of the spectrum in growth and movement. Plants can, however, be grown in considerable ranges of spectral quality, as is shown by the fact that healthy growth may be obtained both in daylight and under electric lamps. The effect on the plant of the change in spectral quality of daylight which occurs on the transition from an unclouded to a cloudy sky, and also with the diurnal variation from sunrise to sunset, is still unknown. With greater knowledge of the biological effect of light of different wave length plant physiologists will no longer be content with a record of total light intensity but will require for work in agricultural meteorology a record of the spectral quality of light in different localities and also a continuous record of the diurnal variation of this quality.

Effect of Humidity of the Air.

The humidity of the air is one of the dominant factors in plant growth and crop yield. Its effect is, of course, largely dependent on the soil moisture available to the plant. The loss of water from the plant, if other conditions remain the same, is directly related to the evaporating power of the air. It is perhaps unfortunate that meteorological records of humidity are usually given in terms of *percentage saturation* of the air, since such data are only comparable among themselves if the temperature is constant. Thus, air having a 70 per cent. saturation at 20° C. and 30° C., respectively, has very unequal evaporating power, for the saturation deficits are 5.22 mm. and 9.47 mm. of mercury in the two cases. From the agricultural standpoint what is required is the "saturation deficit" of the air, for on this depends the water loss from the plant.

Photoperiodism.

Reference must be made to the more recent work of Garner and Allard in America, who have shown that a hitherto unsuspected meteorological condition—namely, length of day—has a marked effect on flower development, and so on crop yield. It is a familiar fact that many plants flower only at certain seasons of the year, such as spring and autumn. It was usually assumed that temperature was the dominant factor, the appearance of spring flowers being associated with the warmth that follows the chill of winter, while autumn flowering seemed to be the result of the decline of temperature as we pass from summer towards winter. Though temperature is certainly a very important factor it is not the dominant one in relation to flowering. One cannot make the iris flower in winter by putting it in a greenhouse, or asters and chrysanthemums flower in summer by lowering the temperature. It is clear that with many plants the time of flowering and fruiting is linked with the season. The clue to the nature of this relationship was gained from a study of a valuable variety of tobacco, Maryland Mammoth,

grown in the United States. This plant when growing in Virginia produces no seed but goes on growing steadily during the season, reaching a height of even 12 ft., till finally it is cut down by frost without flowering. A plant, however, which was placed in a greenhouse in autumn flowered in a short time and set seed. It was at first thought that the effect was one of temperature, but it was soon found that whatever the conditions the plant would never flower in the summer but only in the winter. The time of flowering was shown to be controlled by *length of day*, the tobacco in question being a "short-day" plant which would not flower in the long days of summer. It was later shown that many other plants showed the same characteristic and *could be induced to flower in summer by artificial shortening of the period of exposure to daylight*. The term *photoperiodism* has been applied to this phenomenon, and it is certainly a very striking response of the plant to meteorological conditions. The nature of the action is still obscure, but it would seem evident that the photochemical effects on the plant alter with the duration of exposure, even if the intensity is kept constant.

Conclusion.

The general conclusion may be drawn that the ordinary meteorological data of temperature and humidity are adequate for plant physiological purposes, though soil temperatures as well as air temperatures are required for the fuller study of the plant's reaction to this climatic factor. With regard to light, what is required is a measure of total radiation or, what would be still better, some measure of brightness and its variation during the day. The plant is certainly affected by light quality as well as light intensity, so that as our knowledge increases there will be need for a record at different localities of the energy distribution throughout the spectrum and its changes during the day.

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